

Large scale patterns of forage yield and quality across Chinese grasslands

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Received January 31, 2012; accepted August 27, 2012; published online November 27, 2012

Understanding the patterns of forage quantity and quality and investigating the factors influencing these patterns are essential for the development of animal husbandry. However, there is very little field evidence focused on these issues at a large spatial scale. In the current study, we analyzed forage quantity and quality at 177 sites distributed in all the major grassland types across China, and explored the relationship between forage quantity and quality based on consistent sampling protocols. We also investigated potential factors influencing forage quality patterns across China. Our study indicates the Tibetan grasslands had both higher quantity and quality forage than the Inner Mongolian grasslands, and alpine meadow had the best quantity and quality forage because of the meadow's high productivity and the crude protein and nitrogen free extract content of the meadow forage. For the main vegetation formations, *Kobresia tibetica* meadows and *Achnatherum splendens* steppes had the highest quantity, while *Kobresia pygmaea* meadows and *Kobresia humilis* meadows had the best quality. We also found that although environmental factors, such as temperature and soil fertility, could affect physiological processes and so influence forage quality, the large scale patterns of change were mainly a result of the differences in vegetation types. Finally, we reported a negative relationship between forage quantity and quality: higher forage quantity means more crude fiber but less ether extract and crude protein. These findings improve our understanding on the spatial patterns of forage quantity and quality, and provide solid evidence related to the future development of animal husbandry.

alpine grassland, development of animal husbandry, grassland quality, temperate grassland

Citation: Shi Y, Ma Y L, Ma W H, et al. Large scale patterns of forage yield and quality across Chinese grasslands. Chin Sci Bull, 2013, 58: 1187–1199, doi: 10.1007/s11434-012-5493-4

Grasslands, totaling 3.42×10^9 ha, are one of the most widespread ecosystems worldwide, covering nearly 25% of the earth's land surface [1]. Meanwhile, grasslands are of vital importance for raising livestock and producing animal products [2–4]. China's grasslands, from the Northeast Plain towards the westernmost part of the country, have a total area of 4.0×10^8 ha and cover approximately 33.6% of China's territory [5,6], providing a solid foundation for live-

stock production. However, as a result of long-term unsustainable exploitation and especially overgrazing in the last 50 years, most of China's grasslands are suffering from various degrees of degradation, which not only strongly endangers the development of a pastoral economy, but also threatens the ecological stability of the entire country [7]. Faced with this situation, relevant scientific evidence is critically needed to help land managers charged with revising policies and management strategies, in their efforts to guarantee the proper use of grasslands and sustainable development of the livestock industry.

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Forage quantity and quality are usually considered the most important indices for grassland resource assessment: forage quantity, a measurement of grassland productivity as well as the quantity of dry matter made available to be consumed by livestock, determines the carry capacity of the rangelands; the quality of forage produced by a community mainly influences digestibility and efficiency of the use of digested nutrients, thus affecting livestock performance [8–12]. Therefore, exploring the patterns of forage quantity and quality and investigating the factors influencing these patterns would be of the utmost importance for the scientific management of rangelands and the sustainable development of animal husbandry [13,14].

Until now, through several approaches such as transect surveys, remote sensing and ecological model simulation, Chinese researches have devoted a great amount of effort to investigating the patterns, dynamics and factors influencing grassland productivity in China at local, regional and national scales [15–21]. However, these studies rarely focused on the nutritional value of forage dry matter; thus they might be insufficient as a reference when making scientific policies and management strategies related to animal husbandry. Some uncertainties also exist in studies of forage quality. For example, the classical monograph “Rangeland Resources of China” [6] reported the national-scale patterns of forage quality, but it is based on the national grassland resource survey completed during the early 1980s, and mainly focused on the patterns; recent research studies which analyzed forage quality from individual to community levels were mostly conducted at specific sites, and cannot adequately represent the large-scale distribution and factors influencing forage quality [14,22–24]. Hence, for evaluating the animal husbandry potential in China’s natural grasslands and improving the scientific management and use of rangelands, it is very necessary to investigate the spatial patterns of forage quantity and quality as well as to explore the factors influencing them based on recent large-scale field surveys.

In this study, we analyzed forage quantity and quality data of 528 plots from 177 sites which obtained from a regional field surveys across grasslands on the Inner Mongolian Plateau and the Tibetan Plateau, from two major pastoral areas in China, during 2004–2007. We (1) explore the general patterns of forage quantity and quality across the Inner Mongolian and Tibetan grasslands, (2) compare forage quantity and quality among different vegetation types, (3) attempt to detect the effect of climate and soil on the large-scale patterns of forage quality, and (4) investigate the possible relationships between forage quantity and quality at a large spatial scale.

1 Materials and methods

1.1 Study area

This study was conducted in temperate grasslands on the

Inner Mongolian Plateau and alpine grasslands on the Tibetan Plateau during expeditions in 2004–2007. We set up a grassland transect about 4000 km long that covered grasslands in Gansu and Ningxia, as well as in Inner Mongolia, Qinghai and Tibet (longitude 90.80°–120.12°E, latitude 30.31°–50.19°N stretching from southwest to northeast) at altitudes from 557 to 5105 m a.s.l. for vegetation and soil sampling. Along this transect, growing season temperature (GST, from May to September) and growing season precipitation (GSP) ranged between 11.2–17.6°C and 110–343 mm in the temperate grasslands (107.26°–120.12°E, 38.41°–50.19°N, and 557–1542 m a.s.l.) respectively, and ranged between 2.5–11.4°C and 198–506 mm in the alpine grasslands (90.80°–102.89°E, 30.31°–34.97°N, and 2925–5105 m a.s.l., respectively). The sites along the transect represent natural zonal grassland vegetation, including the five main vegetation types: meadow steppe, typical steppe, desert steppe, alpine steppe and alpine meadow (Figure 1) [25].

1.2 Forage quantity and quality survey

During three summers (late July to early August) of 2004, 2006 and 2007, we visited 131 sites across the transect to collect samples, of which 46 sites were resurveyed in 2007. Considering the probable interannual variation, all revisited sites were treated as new sites; thus a total of 177 sites were sampled (meadow steppe, 9 sites; typical steppe, 54 sites; desert steppe, 33 sites; alpine steppe, 18 sites; alpine meadow, 63 sites).

Field sites were selected by visual inspection of the vegetation, with the goal of selecting sample sites subjected to minimal grazing and other anthropogenic disturbances. At each site, we established a 10 m×10 m quadrat randomly and placed three plots (1 m×1 m) along the diagonal line of the quadrat. To eliminate the influence of previous harvest, when resampling the same site a second time we located quadrats away from the previously visited microsites. We harvested the aboveground biomass in all three 1 m×1 m plots to ground level. The harvested above-ground biomass was pre-dried in the field using a portable oven and dried to a constant at 65°C after return to the laboratory; then the biomass was weighed to the nearest 0.1 g.

After biomass measurements, the samples were ground using a ball mill (NM200, Retsch, Germany) for determination of forage quality. We obtained forage quality using a proximate analysis system (Weende system), which divided the dry matter into crude protein (CP), crude fiber (CF), ether extract (EE), nitrogen-free extract (NFE), and ash (only measured for calculating NFE and not analyzed further) [26]. The analysis of forage quality was conducted in the laboratory at China Agricultural University, Beijing.

1.3 Climate and soil data collection

Climate data used in this study included mean annual tem-

perature (MAT), mean annual precipitation (MAP), GST and GSP. These data were compiled from the 1950–2000 temperature/precipitation records in a global climate database with a spatial resolution of 0.0083° [20,27].

Soil data were obtained from soil samples from each site. The sampling was split into two parts: schematic soil sampling by drilling at depth increments (0–5, 5–10, and 10–20 cm) for chemical analyses, as well as volumetric sampling using a standard container (100 cm³ in volume) at equal depths for soil bulk density (SBD). The sampling protocol and analysis for soil organic carbon (SOC), SBD, soil total nitrogen (STN), soil total phosphorus (STP), and soil available phosphorus (SAP) have been detailed previously [28,29].

1.4 Statistical analyses

We carried out independent-sample *T*-tests to compare the effects of region on forage quantity and quality. One-way ANOVA with Turkey's *post hoc* test was conducted to explore the differences of forage quantity and quality among 5 vegetation types and 9 major vegetation formations. Pearson correlation analysis was used to detect the relationships between forage quality and environmental factors. Since environment might influence forage quality indirectly through differences in the vegetation types, we carried out analysis of covariance (ANCOVA) to test the changes in the rela-

tionships between environmental factors and forage quality among five vegetation types. Based on the ANCOVA results, we built a linear multivariate regression model to investigate the effects of climate and soil properties on forage quality. Finally, correlation analysis was conducted to explore the possible relationships between forage quantity and quality.

Forage quantity data were log transformed to achieve a normal distribution (Figure 2). Because the sampling intensity of meadow steppe might be slightly weak, all analyses except descriptive statistics were based on plot-level data.

All statistical analyses were performed using SPSS v.18.

2 Results

2.1 Patterns of forage quantity and quality

Histograms of forage quantity and four indices of forage quality were prepared (Figure 2). As illustrated, large differences existed across all surveyed plots for forage quantity, CP, CF, EE and NFE (Table 1).

Forage quantity and quality also showed apparent regional variation (Figure 3). Forage quantity of the Tibetan alpine grasslands (115.0 g m⁻²) is significantly higher than in the Inner Mongolian temperate grasslands (79.8 g m⁻²). For forage quality, Inner Mongolian temperate grasslands had higher EE (3.22%) and CF (24.65%), while Tibetan alpine

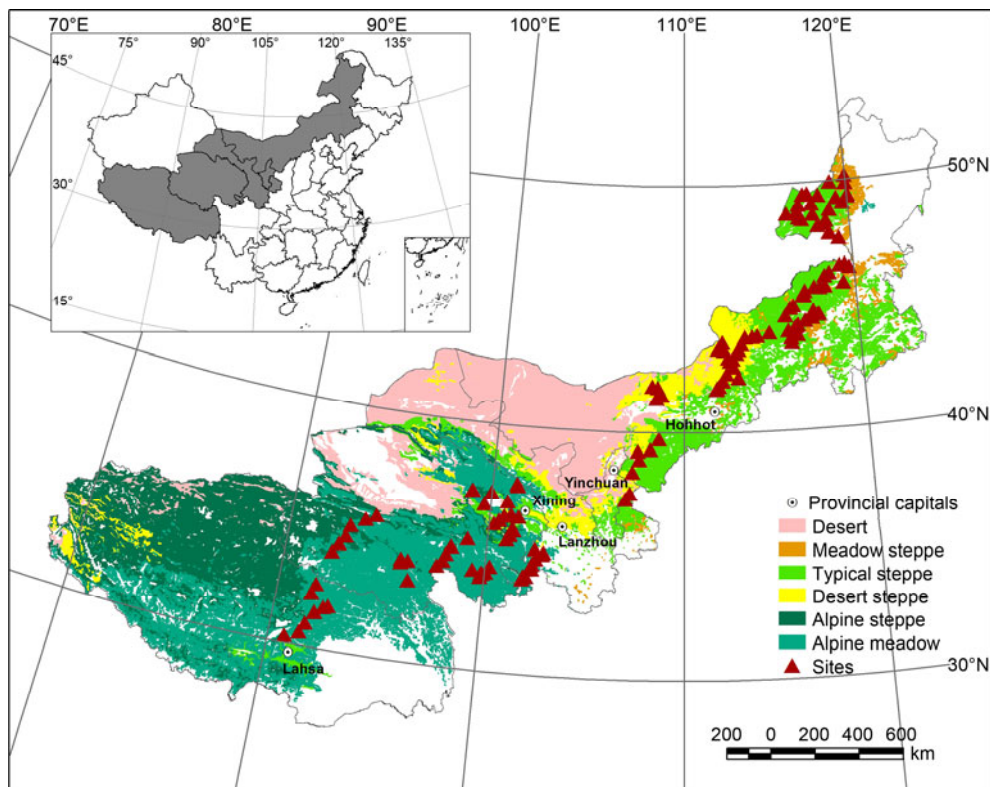


Figure 1 Geographical distribution of sample sites on a vegetation map background (1:1000000).

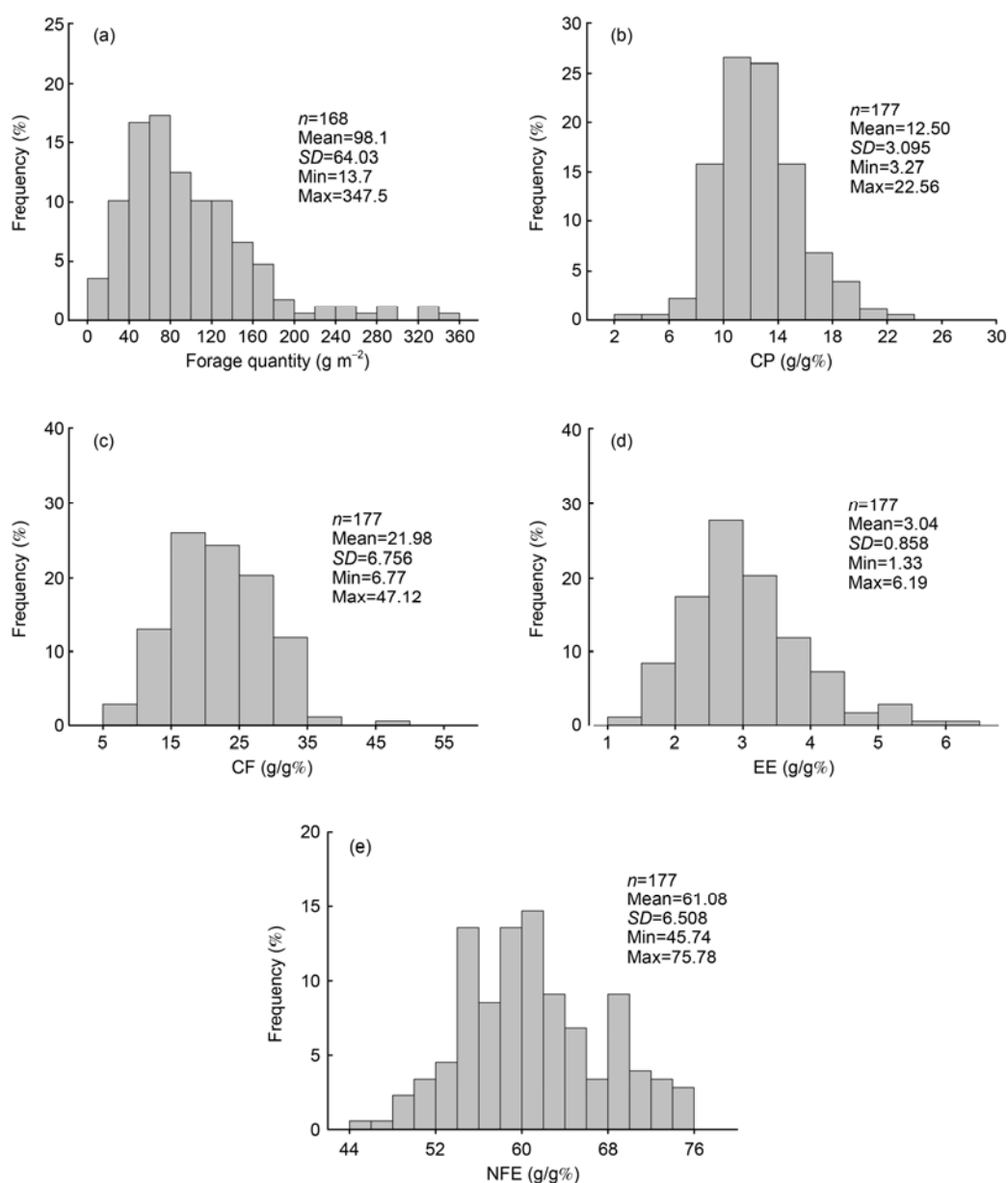


Figure 2 Frequency distributions of forage quantity (a), CP (b), CF (c), EE (d) and NFE (e). The distribution of forage quantity has no significant differences compared with the log-normal distribution at $P<0.05$, while other distributions have normal distributions.

grasslands were richer in CP (12.87%) and NFE (63.53%).

2.2 The differences of forage quantity and quality among vegetation types

One-way ANOVA analysis shows forage quantity and quality varied obviously among different vegetation types (Table 1). Forage quantity in alpine meadows and meadow steppes was higher while it was lower in desert steppes and alpine steppes. For forage quality, different types of nutrient content show different trends: CP was higher in alpine meadows, desert steppes and alpine steppes, and lowest in meadow steppes; CF was relatively higher in all temperate grassland types, but

lower in the two alpine grassland types; EE was higher in desert steppes and alpine steppes and lower in alpine meadows and meadow steppes; NFE content was higher in alpine meadows, alpine steppes and meadow steppes, while lower in desert steppes.

We chose *Stipa grandis* steppe, *Stipa krylovii* steppe, *Achnatherum splendens* steppe, *Stipa klemenzii* steppe, *Stipa breviflora* steppe, *Stipa purpurea* steppe, *Kobresia humilis* meadow, *Kobresia pygmaea* meadow and *Kobresia tibetica* meadow, which are widely distributed and for which we also had sufficient data available to compare forage quantity and quality in more detail. The results show forage quantity and quality of the above nine vegetation formations showed

Table 1 Forage quantity, crude protein (CP), crude fiber (CF), ether extract (EE) and nitrogen-free extract (NFE) in 5 vegetation types across the grasslands of the Inner Mongolian and Tibetan plateaus, China^{a)}

		N	Mean	SD	95% lower limit	95% upper limit
Forage quantity (g m ⁻²)	Meadow steppe	27	119.0c	43.10	101.9	136.0
	Typical steppe	152	91.5b	42.03	84.8	98.3
	Desert steppe	99	62.3a	39.60	54.4	70.2
	Alpine steppe	54	61.5a	47.86	48.4	74.6
	Alpine meadow	167	133.9c	86.97	120.6	147.2
CP (g/g %)	Meadow steppe	27	9.68a	2.849	8.55	10.81
	Typical steppe	161	12.15b	2.943	11.70	12.61
	Desert steppe	99	12.97bc	3.707	12.23	13.71
	Alpine steppe	54	12.35bc	3.206	11.48	13.23
	Alpine meadow	185	13.16c	2.913	12.74	13.58
CF (g/g %)	Meadow steppe	27	24.18b	7.250	21.32	27.05
	Typical steppe	161	24.98b	6.895	23.91	26.06
	Desert steppe	99	24.66b	5.884	23.48	25.83
	Alpine steppe	54	18.46a	6.097	16.80	20.13
	Alpine meadow	185	18.15a	5.746	17.31	18.98
EE (g/g %)	Meadow steppe	27	2.66a	0.787	2.35	2.97
	Typical steppe	161	3.05b	0.955	2.90	3.20
	Desert steppe	99	3.42c	1.062	3.21	3.63
	Alpine steppe	54	3.28bc	1.057	2.99	3.57
	Alpine meadow	185	2.84a	0.735	2.74	2.96
NFE (g/g %)	Meadow steppe	27	62.80c	7.025	60.02	65.58
	Typical steppe	161	58.80b	6.985	57.72	59.89
	Desert steppe	99	57.04a	6.186	55.80	58.27
	Alpine steppe	54	63.94a	5.308	62.49	65.39
	Alpine meadow	185	64.45c	5.917	63.59	65.31

a) Sample size (N), mean, standard deviation (SD) and 95% lower and upper limit of observation are shown. Different letters indicate statistically significant differences at $P<0.05$.

significant differences in ways that were similar to the analysis of vegetation types (Figure 4). The *K. tibetica* meadow and *A. splendens* steppe had the highest quantity of forage while *S. breviflora* steppes had the least. For forage quality, *K. humilis* meadow and *K. pygmaea* meadow had relatively higher CP and NFE content but low CF; *A. splendens* steppe and *S. breviflora* steppe had higher CF but lower CP and NFE content. *S. breviflora* steppes and *S. grandis* steppes also had higher EE concentration while *K. tibetica* meadow, *A. splendens* steppe and *K. humilis* meadows were lower in EE.

2.3 The effects of climate and soil factors on forage quality patterns

Regression analysis between CP, CF, EE, NFE and climate factors as well as soil factors (Table 2) identified no significant interaction between climate factors and CP, while the relationships between NFE and all climate factors were sig-

nificant; CF and EE were positively correlated to GST, MAT, GSP and GSP, MAP, GST, respectively. Meanwhile, SOC, STN, SAP and SBD had significant positive correlations to CP, CF, EE and NFE, while STP only had a significant positive relationship with CP.

After eliminating the effect of vegetation types the results of ANCOVA show some environmental factors still had direct effects on forage quality (Table 3): CP was positively significantly correlated to SOC, but negatively to SBD ($P<0.1$); CF was positively significantly correlated to MAT while negatively to STN and STP ($P<0.05$); EE was influenced positively by GST but negatively by SAP, and NFE was positively influenced by STP. Moreover, interaction between climate factors and vegetation types will also exert influence on forage quality: CP was influenced by the respective interactions between MAT, SOC, STP, SAP, SBD and vegetation type ($P<0.05$); For CF, the respective interactions between GSP, MAT, STP, SBD and vegetation type had significant effects ($P<0.1$); EE was related to the

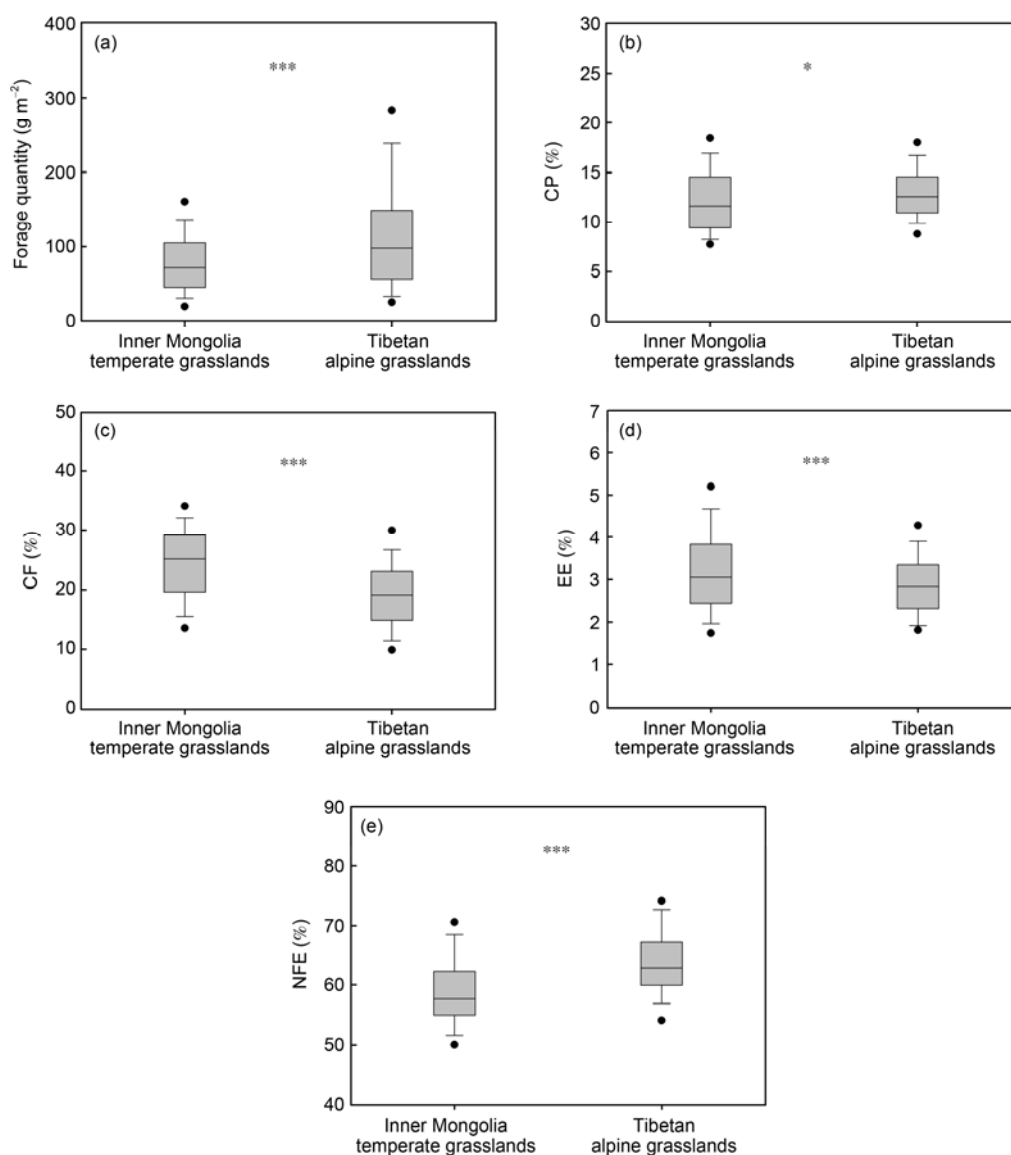


Figure 3 Comparison of forage quantity (a), CP (b), CF (c), EE (d) and NFE (e) between Inner Mongolia temperate grasslands and Tibetan alpine grasslands. ***, $P < 0.001$; *, $P < 0.05$.

interaction between GSP, MAT and vegetation type ($P < 0.05$); NFE, however, was influenced by the interaction between GSP, SBD and vegetation type ($P < 0.05$).

Based on the above results, we established multivariate regression models to check the effect of vegetation type and environmental factors on forage quality at a large scale (Table 4). Considering the differences between different vegetation types, we found vegetation type was the most important explanatory factor for forage quality, explaining 24% ($P < 0.001$), 32% ($P < 0.001$), 11% ($P < 0.05$) and 27% ($P < 0.001$) of the total variances in CP, CF, EE and NFE, respectively. However, although several environmental factors also show significant relationships with forage quality, they could only explain a relatively low percentage of the total variance, with explanatory rates of 3%, 12%, 5% and 4% for CP, CF, EE and NFE, respectively. Additionally,

there exist significant interaction effects between vegetation type and several environmental factors. That is, the effects of some factors vary for different vegetation types (Table 4).

2.4 The relationship between forage quality and quantity

The regression analysis between forage quality and quantity over the entire region surveyed (Figure 5) indicated that across our study region, CP and EE content both had a significant negative relationship with forage quantity, CF had a significant positive relationship with forage quantity, and no significant relationship existed between NFE and forage quantity. In both the Inner Mongolian grasslands and Tibetan grasslands, CP, CF and EE all had similar relationships with forage quantity as those in the entire study region, while the relationship between NFE and forage quantity was

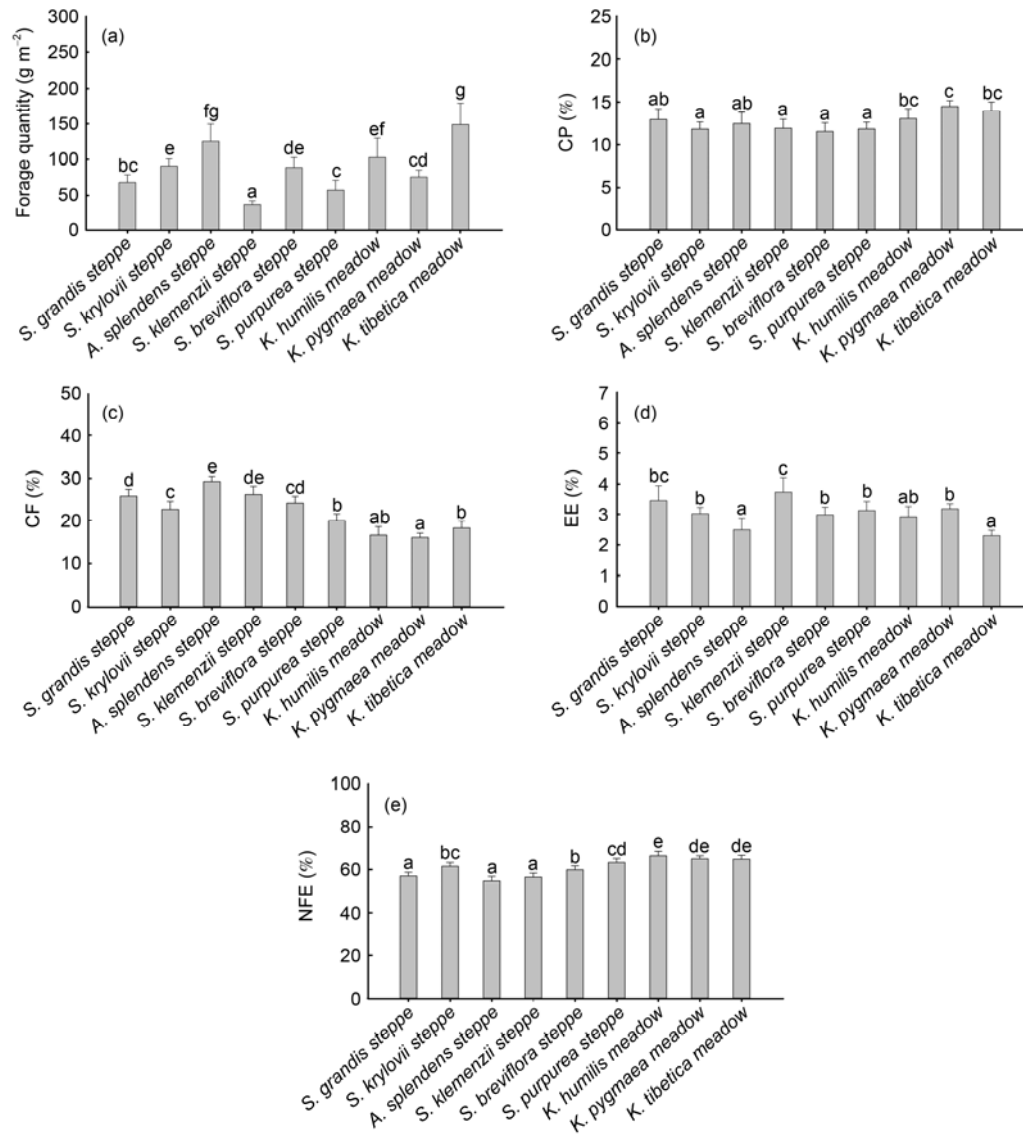


Figure 4 Comparison of forage quantity (a), CP (b), CF (c), EE (d) and NFE (e) between nine major vegetation formations in the study region. Different letters indicate statistically significant differences at $P < 0.05$.

Table 2 Correlation between forage quality and environmental factors^{a)}

		CP	CF	EE	NFE
Climate factors	GST	-0.157	0.378**	0.170*	-0.348**
	GSP	0.069	-0.210*	-0.199*	0.251**
	MAT	-0.162	0.360**	0.066	-0.327**
	MAP	0.001	-0.117	-0.223**	0.193*
	SOC	0.235*	-0.283**	-0.248*	0.242*
Soil factors	STN	0.253**	-0.327**	-0.246*	0.275**
	STP	0.321**	-0.203*	-0.134	0.079
	SAP	0.273**	-0.325**	-0.307**	0.268**
	SBD	-0.224*	0.336**	0.218*	-0.322**

a) The correlation coefficients are provided. GST, growing season temperature; GSP, growing season precipitation; MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SAP, soil available phosphorus. *, $P < 0.05$; **, $P < 0.01$.

Table 3 Summary of ANCOVA for the effects of vegetation type, climate and soil on forage quality^{a)}

		CP	CF	EE	NFE
<i>P</i> value of main effect	VT	0.000**	0.000**	0.065†	0.000**
	GST	0.651	0.453	0.002**	0.961
	GSP	0.22	0.666	0.377	0.75
	MAT	0.125	0.025*	0.14	0.248
	MAP	0.74	0.643	0.73	0.842
	SOC	0.083†	0.487	0.995	0.342
	STN	0.975	0.044*	0.728	0.571
	STP	0.914	0.001**	0.41	0.001**
	SAP	0.363	0.047*	0.021*	0.253
	SBD	0.095†	0.425	0.489	0.384
<i>P</i> value of interaction	GST	0.51	0.985	0.549	0.637
	GSP	0.296	0.053†	0.063†	0.086†
	MAT	0.024*	0.034*	0.010*	0.949
	MAP	0.215	0.147	0.326	0.192
	SOC	0.001**	0.890	0.853	0.293
	STN	0.718	0.500	0.516	0.687
	STP	0.010*	0.038*	0.360	0.142
	SAP	0.022*	0.550	0.260	0.679
	SBD	0.010*	0.041*	0.472	0.017*

a) The significant levels of main effect and interactions are provided. VT, vegetation type. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.1$.

Table 4 Summary of linear multi-variation regression model for the effects of vegetation types, climate and soil on the forage quality^{a)}

Model		SS	SS%	df	F	P
CP~VT+SOC+SBD+VT:(MAT+SOC+STP+SAP+SBD)	VT	173.74	24.19	4	11.40	0.000**
	SOC	12.04	1.68	1	3.16	0.081†
	SBD	11.68	1.63	1	3.06	0.085†
	VT: MAT	85.12	11.85	5	5.58	0.011*
	VT: SOC	59.46	8.28	4	3.12	0.001**
	VT: STP	45.72	6.37	5	2.40	0.015*
	VT: SAP	50.34	7.01	5	3.30	0.048*
	VT: SBD	62.78	8.74	4	3.29	0.017*
	Residuals	217.24	30.25	57		
CF~VT+MAT+STN+STP+SAP+VT:(GSP+MAT+STP+SBD)	VT	1068.97	31.87	4	13.16	0.000**
	MAT	100.08	2.98	1	4.93	0.030*
	STN	4.00	0.12	1	0.20	0.659
	STP	240.84	7.18	1	11.86	0.001**
	SAP	63.82	1.90	1	3.14	0.081†
	VT: GSP	47.67	1.42	5	0.47	0.797
	VT: MAT	254.24	7.58	4	3.13	0.021*
	VT: STP	64.96	1.94	4	0.80	0.530
	VT: SBD	290.87	8.67	5	2.86	0.022*
	Residuals	1218.55	36.33	60		
EE~VT+GST+SA P+VT:(GSP+MAT)	VT	7.98	10.61	4	3.48	0.011*
	GST	0.86	1.14	1	1.50	0.223
	SAP	2.89	3.84	1	5.05	0.027*
	VT: GSP	8.16	10.85	5	3.11	0.013*
	VT: MAP	8.92	11.86	5	2.85	0.020*
	Residuals	46.38	61.68	81		
NFE~VT+STP+VT:(GSP+SBD)	VT	775.12	27.33	4	8.89	0.000**
	STP	115.04	4.06	1	5.28	0.025*
	VT: GSP	87.79	3.10	5	0.80	0.550
	VT: SBD	310.48	10.95	5	2.85	0.021*
	Residuals	1547.88	54.57	71		

a) SS, sum of squares; %SS, percentage of total sum of squares explained. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.1$.

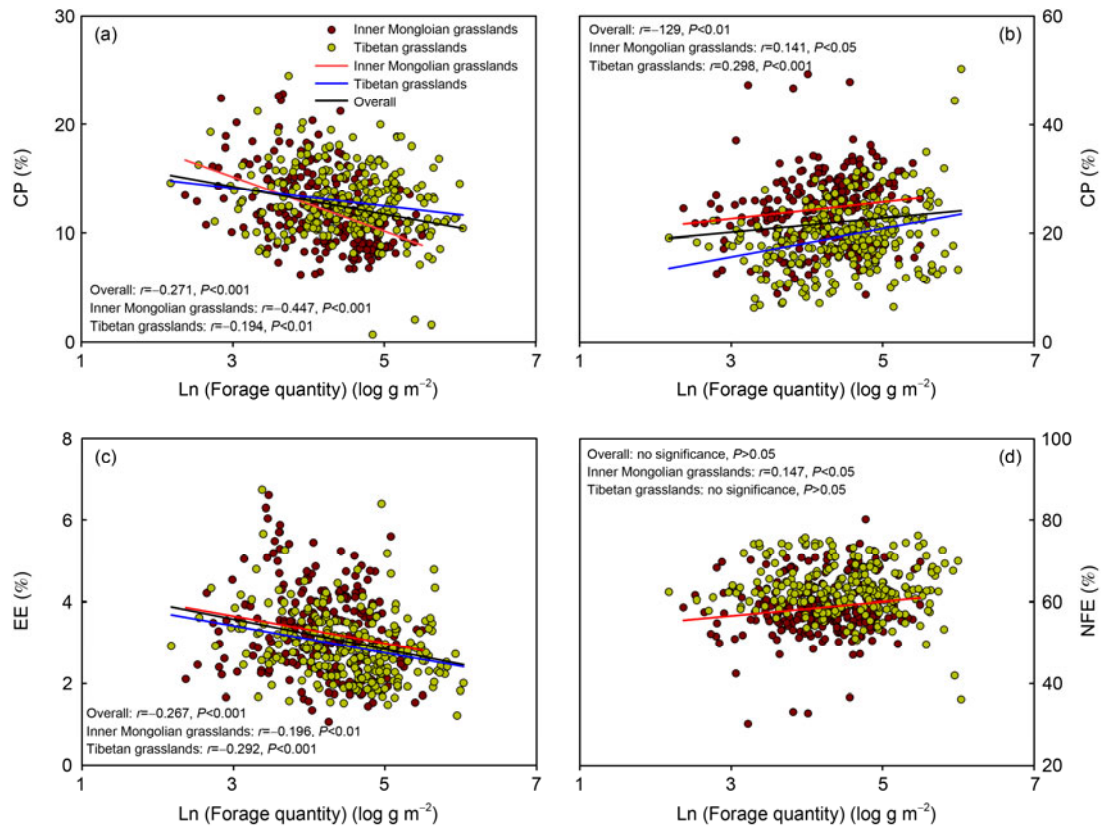


Figure 5 Linear regressions between CP (a), CF (b), EE (c), NFE (d) and forage quantity in the entire study region, Inner Mongolian grasslands and Tibetan grasslands, respectively. Slope, R^2 and P value are provided.

not significant in the Tibetan alpine grasslands but positively significant in the Inner Mongolian grasslands. The analyses in five different vegetation types show: for alpine meadows, CP was negatively correlated with forage quantity, while CF positively correlated with forage quantity, and NFE had no significant relationship with forage quantity; for desert steppes, CP and EE were both negatively correlated with forage quantity, while CF and NFE both had no significant relationship to forage quantity; for typical and alpine steppes, CP was in negatively related to forage quantity but CF was the opposite; For meadow steppes, there were no relationships between any of the nutrient contents and forage quantity (Table 5).

3 Discussion

3.1 Patterns of forage quantity and quality in China's grasslands

Providing high quality forage in large quantities in grassland ecosystems is essential for the development of animal husbandry [30]. Forage quantity is an important yardstick of grassland resources and determines the volume of dry matter available to livestock, tremendously affecting the carrying capacity of grasslands [10,31,32], while forage quality also has important effects on the quantity and quality of the livestock product produced through affecting the digestibility of food as well as the energy intake and nutrient availability

Table 5 Pearson correlation coefficients between forage quantity and quality in five vegetation types^{a)}

	Pearson correlation coefficient between Ln(forage quantity) and quality			
	CP	CF	EE	NFE
Meadow steppe	-0.085	-0.257	-0.202	0.322
Typical steppe	-0.461**	0.273**	-0.001	-0.068
Desert steppe	-0.309**	0.112	-0.394**	0.164
Alpine steppe	-0.290*	0.261†	-0.077	-0.094
Alpine meadow	-0.273**	0.357**	-0.281**	-0.076

a) **, $P < 0.01$; *, $P < 0.05$; †, $P < 0.1$.

for livestock in pasture [8,9,32]. In this study, we acquired a large amount of data on forage quality and quantity through field-sampling combined with laboratory analysis and analyzed the regional and vegetation differences of forage quantity and quality. Based on this information and analysis the relationships between forage quality and forage quantity, we discussed environmental factors in more detail. Therefore, to a large extent this study can offer baseline data and analysis for land managers making rational planning decisions related to animal husbandry at this point in time.

Generally, forage quantity of the Tibetan alpine grasslands is significantly higher than conditions in the Inner Mongolian temperate grasslands. For different vegetation types, alpine meadows and meadow steppes have the highest forage quantity, while desert steppes and alpine steppes have the lowest. In comparing the different formations, *K. tibetica* meadows have the highest forage quantity followed by *A. splendens* steppes, while the *S. klemenzii* steppes have the lowest quantity. These results correspond well with previous studies [20]. The Qinghai-Tibet Plateau has been considered as having low forage quantity because of the cold climate and short growing season [24,33,34]. However, our study shows that although the forage quantity of alpine grasslands is low, alpine meadows do have relatively high forage quantity, which may be a result of the availability of adequate water in alpine meadows.

The analyses on forage quality show that in Inner Mongolian temperate grasslands EE and CF are higher while CP and NFE are lower than in Tibetan alpine grasslands. This seems to contradict previous conclusions stating Tibetan alpine grasslands have high CP, EE and NFE with low CF [24,35,36]. This is because most previous studies made reached such conclusions by comparing the content of the above nutrients to a specific value but not by comparing nutrient levels in different regions. Other studies have proven EE in Tibetan grasslands was lower than Inner Mongolian grasslands [14]. Therefore, from the perspective of spatial variance, Tibetan grasslands have high CP and NFE with low EE and CF.

Usually CP, EE and NFE in pastures have been considered as important nutrients for livestock, so pastures with higher CP, EE and NFE have higher nutrient value in general. However, the opposite is true for CF [1,34,36]. Our study shows that although EE in Tibetan grasslands is a little lower than in Inner Mongolia (10% lower), CP and NFE are higher than in Inner Mongolia (5.4% and 8.5% higher, respectively) and CF is significantly lower than in Inner Mongolia (21.8% lower), proving that grasslands in the Tibetan region have higher nutrient value. Similarly we can conclude the nutrient values of grasses of alpine steppes and alpine meadows are higher than the nutrient value of those of desert steppes and typical steppes. Meadow steppes have the lowest nutrient value. Also, *K. pygmaea* meadow and *K. humilis* meadow have the highest nutrient value, followed by *K. tibetica* meadow. The nutrient value of *S. klemenzii*

steppe and *A. splendens* steppe are the lowest.

It is also important to note the patterns of forage quantity and quality we found in this study is slightly different from those reported in “*Rangeland Resources of China*”, based on the fact that forage quantity per unit area in alpine meadow steppes is merely half of that in temperate meadow steppes, while the forage quality of alpine grasslands is also higher in EE. Such differences may exist because the vegetation-classification methods we used in this study are the same as the methods used by the editorial board of the Vegetation Map of China, which is different from other grassland resources survey methods [6,25]. Moreover, “*Rangeland Resources of China*” was based on the early survey of grassland resources conducted during the 1980s, which was 20 years before our study, which may explain the above differences.

3.2 Effect of environmental factors on forage-quality patterns

The nutrient content of vegetation is partly affected by the intrinsic characteristics of vegetation such as physiological properties and is also partly influenced by local habitat and environmental conditions, which are a result of the interaction between phylogenetic development and environmental factors; specifically, material and energy transformation in plants are determined by both evolutionary and ecological processes [37,38]. Therefore, large-scale forage-quality patterns are inseparable from environmental factors.

Environmental factors play their role partly by affecting the vegetative composition of grasslands. Although regression analysis shows many climate and soil factors were positively correlated with forage nutrient indices, after taking vegetation type into consideration some of them become insignificant. Meanwhile multivariate regression analysis shows the most important explanatory factor for forage quality on a large scale is vegetation type (explaining 10% of the total variance). All these indicate that environmental factors on a large scale exert influence on forage-quality patterns primarily by changing the vegetation type and species composition. Such effects of environmental factors may be correlated with long-term evolution. For example, alpine plant species have evolved a series of adaptive mechanisms in response to long-term exposure to low temperatures. These include decreased structural-carbohydrate content and increased soluble-carbohydrate content as well as increased protein content, which reduces damage caused to the plant by low temperatures; the opposite occurs in warm regions [40,41]. This also explains why in Tibetan grasslands have been observed to have high CP, NFE and low CF.

However, multivariate regression analysis also shows that even after taking vegetation type into consideration some environmental factors still have significant influence on forage quality, which may be caused by the fact environmental factors can affect forage-quality patterns through

certain physiological mechanisms [1,40–42]. From the results of multivariate regression analysis we can see that among all climatic factors only MAT significantly influenced CF, which may reflect the effect of low temperatures during dry matter accumulation in plants. Previous studies show an increase in temperature will result in a decrease of the leaf/stem ratio and will promote the production of structural carbohydrates with an increase in the CF content and a reduced digestibility of pasture forage [42,43], consistent with our results.

All soil nutrient indices positively and significantly influenced forage, which suggests the nutrient condition of the soil affects forage quality more directly than other factors. In particular, CF, EE and NFE are all positively significantly influenced by the phosphorus content of the soil such as STP and SAP (explaining total variance of 9.1%, 3.8% and 4.1% of CF, EE and NFE, respectively). Phosphorus is an element required for plant growth, and an essential component of many chemical substances in plants such as phospholipids, nucleic acids, ATP and NADP, and is closely related to many metabolic processes in plants [44,45]. Nutrient control experiments on rice show that after reducing the phosphorus content of soil, the expression of enzymes related to cell-wall-synthesis increased significantly while the expression of enzymes related to lipolysis decreased [46]. A study of pigeon pea (*Cajanus cajan*) using isotope labeling shows a decrease of soil phosphorus could significantly inhibit the accumulation of non-structural carbohydrates [47]. Previous researchers believed most soils in China are phosphorus deficient [48,49]. Therefore, soil phosphorus may affect forage quality through the physiological processes described above resulting in increased phosphorus demand and consequently an increase in NFE as well as an increase in EE and CF. Apparently, the physiological processes related to how phosphorus demand influences forage quality are still unknown, so additional studies are needed. However, in our analysis the explanatory abilities of environmental factors are quite low. Aside from CF, the explanatory abilities of all remaining nutrient indices are below 10% on a large scale indicating their influence on plant physiological processes are not the main factors driving large scale grassland landscape patterns.

3.3 Relationship between forage quality and quantity

By analyzing the relationships between forage quality and quantity we can see a significant relationship exists between them. As forage quantity increases CF also increases while CP and EE of grass decrease. That is, forage quality decreases as forage quantity increases. Therefore, a negative relationship might exist between forage quality and above-ground biomass.

Such negative relationships seem to contradict the large-scale patterns of forage quantity and quality. However, further analysis shows this relationship exists in different re-

gions. For grasslands with different vegetation types, not all vegetation types show significant relationships between forage nutrient components and forage quantity, but most exhibit a decreasing trend for CP with an increase in forage quantity. Some vegetation types also show the same trend for EE and an opposite trend for CF. All these suggest a negative relationship between forage nutrient value and forage quantity does exist in grasslands. Such relationships on a small scale do not contradict the large-scale pattern, which in essence is synthesized by small-scale relationships.

No previous studies have been conducted related to the negative relationship between forage quality and quantity on a large scale on natural grasslands. Studies of anthropogenic grasslands show such a relationship does exist. White et al. conducted a study of grass and leguminous forage, which indicated forage CP content decreased by 0.80%–1.25% and digestible dry matter also decreased gradually with the increase of forage quantity by 1000 kg/ha [50]. Such trends also exist for both cool- and warm-season forage types [32]. With the increase of forage quantity, both acid detergent fiber (ADF) and neutral detergent fiber (NDF) increase gradually [51,52].

The relationship between forage quality and quantity may be related to the processes involved in the distribution of elemental nutrients during plant growth. From the perspective of ecological stoichiometry, higher biomass of a plant community may have a diluting effect on N and P, which has the effect of diluting the nutrient-element concentration as biomass increases [53–55]. Particularly, this is because as dry matter accumulates a plant's mechanical tissues grow and the proportion of physiologically active non-mechanical tissues gradually declines [56,57]. Since there is little N in mechanical tissues but large amounts of CF such as cellulose and lignin, with the increase of forage quantity CP eventually shows a decreasing trend while CF increases. However, most discussions related to this topic and the mechanism controlling it are based on local-site studies, which are quite different from our study, so additional study is still needed.

3.4 Uncertainty in the study

Temporal dynamics exist for forage nutrients, which may change with the growing seasons [1,14,41]. Limited by the methodology required for large-scale research, both forage quantity and quality were measured in this study derived from the samples collected between late July and early August. Samples from different stages of the growing season were not collected. Thus the patterns of forage quality and quantity together with the factors influencing them may change at different stages of the growing season. The dynamics and factors influencing such patterns still need further study. Also, because of limits to objective conditions such as time, manpower and materials, an analysis of detailed nutrient components of each species was not con-

ducted but only general data related to grasslands were collected. Although different vegetation types were taken into consideration when analysis was conducted, based on the percentage of error sum squares in the multiple regression models, variance caused by species composition may still exist. General nutrient measurements for grasslands do not provide sufficient data to calculate the construction cost, so the mechanisms driving forage-quality patterns still need additional discussion. Also, because meadow steppes cover relatively small areas, the number of meadow steppe sites is a little small compared to other vegetation types. Although plot level data were used to enhance the reliability of the statistical analysis, errors resulting from low sampling intensity could still not be fully excluded.

Such limitations deserve further discussion. If one considers the different forage species from the perspective of the construction cost for aboveground organs and the effects of environmental factors, this information may help us understand the causes of the formation of various forage quality patterns on a large scale. Moreover, long-term observation of a series of plots along environmental gradients will help us to discuss forage quality patterns in different stages of the growing season; meanwhile these data may help us conduct further field controlled experiments to investigate mechanisms related to the relationships between environmental factors and forage quality.

4 Conclusion

Through analyzing the forage quantity and quality of 177 sites distributed in all the major grassland types across China, the current study explored large-scale patterns of forage quantity and quality, and investigated the environmental factors that determine them.

Our study indicated, in general, the Tibetan grasslands had both higher forage quantity and quality than the Inner Mongolian grasslands, and alpine meadow had the best quantity and quality because of its high productivity and content of CP and NFE. For the main vegetation formations, *K. tibetica* meadows and *A. splendens* steppes had the highest quantity forage, while *K. pygmaea* meadows and *K. humilis* had the best quality. We also found that although environmental factors, such as temperature and soil fertility, could affect the physiological processes and thus influence forage quality, the large-scale patterns would be mainly a result of the presence of different vegetation types. After eliminating the effect of vegetation type, only CF was affected by a climate factor, MAT, while all four forage quality indices were influenced by soil factors. In particular, the significant influences of soil phosphorus on CF, EE and NFE might suggest a greater shortage of soil phosphorus in China's grasslands. Finally, a negative relationship was found between forage quality and quantity: higher forage quantity means more CF, but less CP and EE. This may

indicate the dilution process of nutrients with the accumulation of biomass.

We thank the members of the Peking University Sampling Campaign Teams to the Tibetan Plateau and the Inner Mongolia Autonomous Region for their assistance in field investigations. We also thank Professor Zhongling Liu, Inner Mongolia University, for assistance with plant species identification in the field, and Professor Liping Ren, China Agricultural University, for assistance in laboratory analyses. This study was supported by the National Natural Science Foundation of China (31025005 and 31021001) and the Program of "One Hundred Talented People" of the Chinese Academy of Sciences (KSCX2-YW-Z-0806).

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